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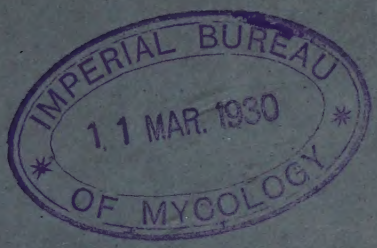

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BREEDING RUST RESISTANT VARIETIES OF WHEAT—FUNDAMENTAL ASPECTS OF THE PROBLEM.*

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INTRODUCTION

Concurrently with attempts to breed rust resistant varieties of wheat certain fundamental investigations bearing on the entire problem have been conducted. As in all other lines of endeavour we progress only in so far as we understand the principles with which we are dealing. It is therefore of great interest with respect to the problem of breeding rust resistant wheats to examine the results which have been obtained from the fundamental investigations and especially to consider how this knowledge is of direct assistance in the practical breeding work.

CYTOLOGICAL STUDIES

In the first place it was observed that resistance to rust was possessed almost entirely by wheats of the durum and emmer group which are of much less value from the commercial standpoint than the *vulgare* or common wheats. With rust resistance located in one species and commercially desirable characters in another it was evident that interspecific crosses must be made. These crosses however were found to be highly sterile and at first very little progress was made. A very great deal of light was then thrown on this phase of the work by cytological investigations dealing chiefly with the chromosome numbers of the different wheat species and with chromosome behaviour in crosses of species having different numbers. These studies have been conducted chiefly by Sakamura (*21*), Sax (*22*), Kihara (*11, 12*), Thompson (*25, 26, 27, 28*), Thompson and Hollingshead (*29*), Melburne and Thompson (*15*) and Watkins (*30, 31, 32, 33, 34*). It is impossible at this time to go into the cytological work in detail and it will serve the purpose of this discussion to mention a few of the outstanding points.

First, the different wheat species were found to have different numbers of chromosomes. We have the following groups, as shown in table 1, according to chromosome number.

TABLE 1. *Groups according to chromosome number of Triticum species.*

Group	Species	Diploid chromosome number
Einkorn	*Triticum monococcum*	14
	" *aegilopoides*	
Emmer	*Triticum dicoccoides*	28
	" *dicoccum*	
	" *turgidum*	
	" *polonicum*	
	" *durum*	
	" *persicum*	
Spelt	*Triticum spelta*	42
	" *vulgare*	
	" *compactum*	

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The workers mentioned above have followed out the chromosome behaviour in many combinations of these species but we are chiefly concerned here with chromosome behaviour in crosses between varieties of the second and third groups. The crosses studied have been chiefly *dicoccum* × *vulgare* and *durum* × *vulgare*. The typical behaviour may be described briefly as follows. In the gametes of the *vulgare* parent 14 chromosomes out of the 21 appear to be homologous with the 14 chromosomes of the durum or emmer parent and in the first meiotic division of the F_1 plants these pair up and form 14 bivalents. The halves of the bivalent chromosomes separate and go to opposite poles. The remaining 7 of the *vulgare* chromosomes do not find mates in the first division and are therefore termed univalents. These divide equationally in the first division and are distributed at random in the second division.

The essential feature of this chromosome behaviour is the normality of the behaviour of the 14 bivalents, and the distribution of the univalents. As a result of the latter, gametes are produced by the F_1 interspecies hybrid which contain from 14 + 0 to 14 + 7 chromosomes — the extra chromosomes over and above 14 depending on the number of univalents that go to the pole from which the cell nucleus is formed. If the distribution of univalents is random the gametes with an intermediate number of chromosomes will occur most frequently and if these are all viable the great majority of fertilizations will result in zygotes having chromosome numbers intermediate between the parents. Exactly the reverse is true however and we find that in the F_2, plants with chromosome numbers approaching or the same as the parents are found most frequently. The cause of this has been studied in great detail and is now attributed chiefly to (1) gametic sterility (2) zygotic sterility and (3) chromosome loss in the reduction divisions. The gametes with intermediate chromosome numbers in general do not accomplish fertilization so that most of the zygotes result from combinations of 14 + 14, 14 + 21, and 21 + 21, chromosomes. The 14 + 21 combination of course gives plants which closely resemble the F_1 with 35 chromosomes. Some gametes with chromosome numbers approaching the parental ones such as 14 + 1, 14 + 2, and 14 + 5, 14 + 6, do function but an additional factor complicates matters here in that certain zygotic combinations are sterile. That is, certain combinations of say 38 chromosomes are fertile while others of the same number are sterile. The sterile combinations are frequently quite lethal and either do not grow at all or develop into very weak plants which do not set seed. It has also been observed that more F_2 plants from an interspecific cross resemble the parent of lower chromosome number than the parent with the higher number. This is attributed to the loss of univalents in the reduction divisions. These frequently lag on the equatorial plate and do not reach the poles in time to be included in the daughter nuclei.

The sum total of this work in its bearing on the practical breeding problem may be stated as follows. The normal behaviour and pairing of 14 pairs of chromosomes in interspecific crosses must result in an interchange of factors by the usual processes of chromosome segregation and crossing over. Assuming that these chromosomes are homologous the *vulgare*

characters must be due chiefly to the extra 7 pairs but there is considerable evidence that the extra 7 are not entirely responsible for the differences between *vulgare* and durum or emmer varieties. In the homologous 14 group there must be some factor differences and through the process of segregation certain of these factors from the durum or emmer parent can be transferred to types possessing 42 chromosomes. It also seems unreasonable to expect that groups of characters or those single characters dependent upon several factors may be transferred easily. It is logical to expect that rust resistance may be transferred and this is borne out by genetic experiments.

Inheritance of Rust Resistance in Interspecies Crosses

In three cases it has been definitely proved that rust resistance can be transferred from the 28 to the 42 chromosome group. In two well known papers Hayes, Parker and Kurtzweil (*8*), and Hayes, Stakman, and Aamodt (*9*) it was shown that rust resistance had been transferred in a cross of the durum wheat Iumillo with Marquis, to a common wheat. This cross resulted in the production of the variety Marquillo which is highly rust resistant, has 42 chromosomes and is distinctly a *vulgare* type.

From a cross between Yaroslav Emmer and Marquis, McFadden (*14*) obtained the two strains H-44-24 and Hope which are very highly rust resistant and are of the common wheat type. These wheats are practically immune under field conditions and constitute one of the most decided advances in rust breeding work.

At the Dominion Rust Research Laboratory a cross was made in 1925 between Marquis and a durum wheat known as Pentad which is highly rust resistant but of very little commercial value. A hybrid has been produced from this cross which possesses the Pentad type of resistance in the field and is a beardless *vulgare* wheat.

These three are outstanding examples of the transfer of rust resistance from one wheat species to another with a higher chromosome number. The actual ratios obtained are very complicated owing to irregularities in chromosome behaviour and indicate very little with respect to the factorial basis of resistance in such crosses. The fundamental point however is that, as indicated in the first place by the cytological evidence, the resistance can be transferred, and this provides a very firm foundation for practical breeding operations. Evidently the initial step and the most difficult one is the making of interspecific crosses in order to obtain resistance in *vulgare* wheats. These may then be made use of in further crosses in order to combine resistance with quality and other desirable agronomic characters.

Breeding for Resistance to Specific Physiologic Forms of Stem Rust

Aamodt (*2*) has pointed out in an excellent review of the rust breeding work that a great difficulty encountered in the early investigations was the failure of some varieties and new productions to maintain their resistance from year to year and in different localities. This phenomenon was fully explained by the discovery by Stakman and Piemeisel (*23*) in 1917 of the existance of physiologic forms of *Puccinia graminis tritici*. It was evident that most varieties were resistant to certain forms only, and if other forms

appeared in different years or localities the varieties would be susceptible. The collection, identification, and culture of these forms, has been going on continuously since their discovery and reports have been given from time to time by Stakman and Levine (*24*), Newton (*16*), Newton and Johnson (*17*), Newton, Johnson and Brown (*19, 20*), and Levine (*13*). These reports show that we now have approximately 50 forms of wheat stem rust all of which have to be contended with in the breeding program.

The next step in fundamental investigation was therefore the determination of the mode of inheritance in wheat crosses of resistance to particular physiologic forms. Numerous crosses were made. Aamodt (*2*) summarizes the results of these studies as follows—"This evidence as well as that from extensive breeding studies conducted under field conditions substantiates the belief that it is entirely possible to produce a bread wheat resistant to all of the known physiologic forms of rust." In every case it was found that the reactions of the parent varieties to particular physiologic forms could be placed on a definite factor basis—that the resistance of one variety could be combined with the agronomic characters of another variety or that the resistance of two varieties to different physiologic forms could be combined in one variety. Of particular interest from this standpoint is the inheritance of resistance to groups of physiologic forms. The reactions of varieties to such groups of forms are frequently controlled by the same genetic factors. For example Kanred wheat is immune to 11 physiologic forms and it was demonstrated by Aamodt (*1*) that this immunity to 11 forms is controlled by a single genetic factor. In 1928, Goulden, Neatby and Welsh, (*6*) studied a similar relationship in an H-44-24 × Marquis cross and found that the moderate resistance of H-44-24 in the seedling stage to at least five forms was controlled by the same genetic factors. These are allelomorphic to factors in Marquis which gave susceptibility to four of the forms and high resistance to the other. Obviously this mode of inheritance greatly simplifies the breeding problem. Extensive experiments are now being conducted at the Dominion Rust Research Laboratory in order to determine the genetic basis of rust resistance in as many varieties as possible. A complete knowledge of this subject will enable the plant breeders to make appropriate crosses for building up resistance to all of the known physiologic forms.

An important development in our knowledge of the rust problem has come through a study of mutations in physiologic forms and the discovery of heterothallism in the rust organism. Newton and Johnson (*18*) discovered very distinct color mutations in two common physiologic forms. There was very little evidence of a corresponding change in pathogenicity as the forms remained practically the same in their reactions on the differential host varieties, but the fact of mutability is a general indication that changes in pathogenicity may occur and if so the number of forms may be subject to a gradual increase. However we have no direct evidence of this as yet so it does not seem likely that a sufficient number of new forms will arise to interfere seriously with the breeding program. Of distinctly great importance however was the discovery by Craigie (*4, 5*) of heterothallism and the function of the pycnia in the life cycle of the rusts. It was clearly shown that a mechanism exists for crosses between different forms while on the barberry bush and consequently for the production by hybridization of

entirely new forms. Speculating as to the possibilities here we must appreciate first that the forms are quite well mixed in their occurrence throughout the rust area and also in the infections on barberry bushes. It seems likely therefore that most of the possible combinations through hybridization now exist and that new forms can only occur when they arise by mutation and begin to hybridize with some or all of the others. As stated above new mutant forms are not likely to occur frequently but one new mutant form by hybridization with the old ones would result in the production of several distinctly new forms.

Mature Plant Resistance

The alarming possibilities from the production of new forms of rust are very largely offset by the knowledge that a type of resistance exists in some varieties of wheat which seems to apply equally under field conditions to all forms.

It was observed at the Minnesota Experiment Station that some varieties such as Acme, Kota, Velvet Don, and Pentad were quite susceptible to a number of physiologic forms in the seedling stage but were uniformly resistant from place to place and from year to year when grown in the field. It seemed likely that some development took place in the plant as it approached maturity which was responsible for the resistance exhibited at the heading stage. Hursh (*10*) obtained some evidence that this resistance was morphological in nature. This would explain of course why the particular type of resistance should appear to apply equally to all forms of rust. Hayes et al (*9*) in a cross of (Marquis × Iumillo) with (Marquis × Kanred) came to the conclusion that the genetic factors for the resistance of the (Marquis × Iumillo) parent under field conditions were inherited apparently independently from the factors for immunity from certain physiologic forms in the seedling stage. This indicated that the two types were distinct and such a conclusion is amply borne out by the results from two crosses made at the Rust Research Laboratory. The first of these is the H-44-24 × Marquis cross which was reported on in 1928 by Goulden, Neatby and Welsh (*6*). The H-44-24 parent was found to be resistant in the seedling stage to two groups of forms including 21 and 36. All lines of the F_3 generation were tested to these two forms and their reactions were compared with those obtained in the field. The results are best shown in summary form by comparing the field reactions of lines breeding true for seedling resistance with lines breeding true for seedling susceptibility. This is shown in table 2.

Table 2. *Two by three fold contingency table summarizing field reactions of lines homozygous resistant, and homozygous susceptible in the seedling stage.*

Seedling reaction	Field reaction	Homozygous Resistant	Segregating	Homozygous Susceptible	Totals
Resistant to forms	36, 21	8	18	10	36
Susceptible to forms	36, 21	6	18	8	32
Totals		14	36	18	68

$\chi^2 = 0.275$ P = .90 to .80

Here we note that in both groups according to seedling reaction there is a 1 : 2 : 1 ratio in the field of resistant, segregating, and susceptible lines. This proves that the segregation for field reaction is quite independent of the seedling reaction. The same result is illustrated in figures 1 and 2. In figure 1 are shown the seedling reactions of three strains from H-44-24 × Marquis to form 36 and in figure 2 we have the field reactions of the same strains where form 36 was undoubtedly present.

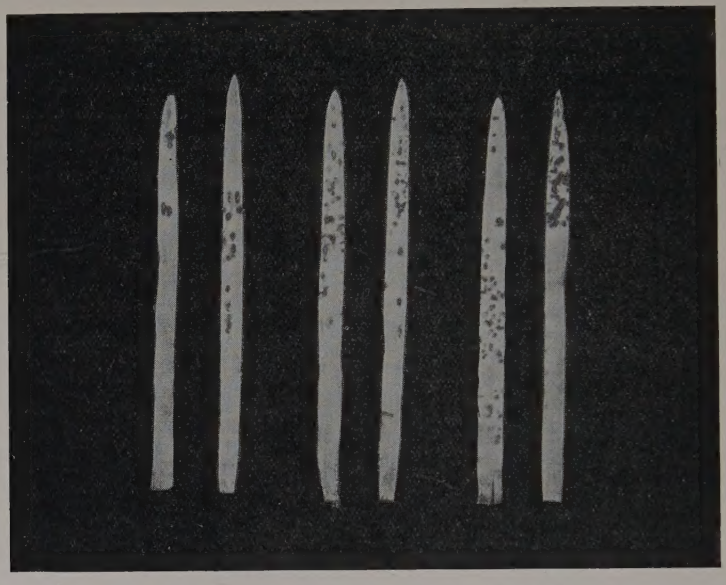

Figure 1. Seedling reactions of three F_3 lines from H-44-24 × Marquis to form 36.

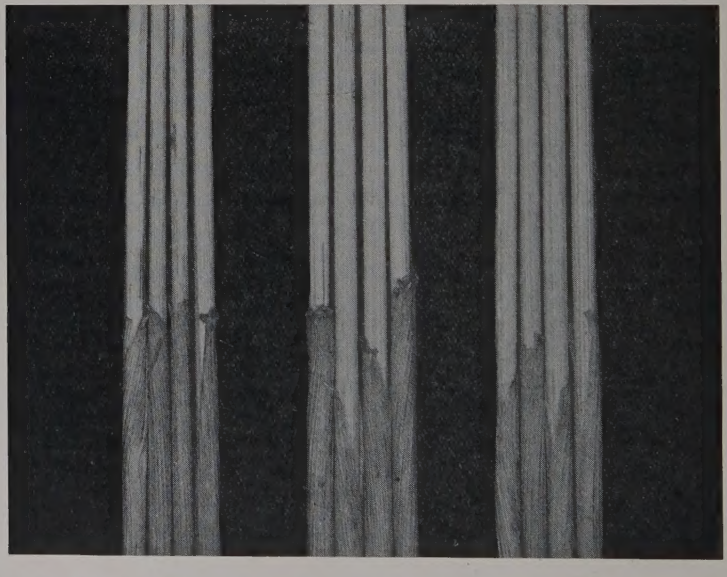

Figure 2. Field reactions of the same three lines illustrated in figure 1.

A result similar to the above has been obtained recently in a Pentad × Marquis cross. The seedling reactions of these two varieties are shown in table 3 as taken from Newton, Johnson and Brown (*19*). Marquis, it will be observed, is susceptible in the seedling stage to most of the forms and it is well known that Marquis is susceptible in the field. Pentad, while highly resistant to a number of forms in the seeding stage, is also fairly susceptible to such forms as 21, 27, 34, 53, and 57. Of these form 21 at least is quite common but Pentad is always highly resistant in the field. It appears, therefore, to possess a high degree of mature plant resistance.

The cross was made in 1925 and from the F_2 grown in 1926 16 plants were saved which were resistant and chiefly of the *vulgare* type. Among the F_3 lines 3 bred true for resistance while two lines segregated according to a 3 : 1 ratio of resistant to susceptible plants. These ratios are given in table 4.

TABLE 3. *Seedling reactions of Marquis and Pentad to 22 physiologic forms.*

	Physiologic forms										
	9	14	15	16	17	19	21	27	29	30	32
Marquis	4—	2—	4—	2=	4—	2—	4	2	4—	4	4=
Pentad	3—	3±	2±	3+	3±c	3±c	3±	4	0;	0;	0;
	33	34	35	36	38	48	49	50	52	53	57
Marquis	2	4—	4=	4	2=	1	4—	2—	4	2±	4
Pentad	x—	4	x±	0;	1±	0;	x	1+	0;	3+	3+

TABLE 4. *Segregation in the field for resistance and susceptibility of two F_3 lines of Marquis × Pentad.*

Line number	Number of Plants Resistant	Susceptible	Total	X^2	P
C—25—F_3—2	125	39	164	.1301	.70
C—25—F_3—8	106	25	131	2.4453	.10
Total	231	64	295	2.5754	.30

The table also shows the values of χ^2 and P for the individual ratios and for both ratios considered together. It is evident that the fit to a 3 : 1 ratio is reasonably good, and indicates that the two F_2 plants giving rise to these F_3 families were heterozygous for a single factor pair.

In order to determine the relation in this cross between seedling and field resistance the progeny of the 125 resistant plants from line C-25-F_3-2 were tested in the seedling stage to form 36 to which Pentad is highly resistant. All of the progenies proved uniformly *susceptible*. In order to obtain additional data on this phase a study was made of a random sample of 12 F_4 lines. These were grown from the 125 resistant plants obtained in 1926 from line C-25-F_3-2, and their progenies were tested in the seedling stage to four forms, 48, 14, 52, and 36. To form 14, Marquis is resistant and Pentad susceptible. To forms 52 and 36, Marquis is susceptible and Pentad highly resistant. To form 48 both varieties are resistant. The results from these tests are given in table 5.

The result is quite striking. It shows that the 12 lines which are uniformly resistant in the field appear to have the Marquis factors for rust reaction in the seedling stage. There is no trace of the Pentad factors for seedling resistance.

TABLE 5. *Seedling reactions to forms 48, 14, 52, and 36 of twelve F_5 lines of Pentad × Marquis which are highly resistant in the field.*

Line No.	Reactions to Physiologic Forms			
	48	14	52	36
1322	1+	1+	4+	4
1324	1+	1—	4+	4
1326	2—	1	4+	4
1335	2—	1±	4+	4
1342	1+	1+	4+	3+
1344	2	2—	4+	3+
1347	1	1	4	4
1350	1	2—	4	3+
1352	2—	1	4—	4
1354	1+	1	4	3+
1355	2—	1	4	3+
1358	1	1	4	3+

This result in addition to the data from the H-44-24 × Marquis cross establishes beyond doubt the independence in inheritance of mature plant and seedling resistance. It is also of great interest to note in both cases that the inheritance of mature plant resistance is very simple. Resistance is dominant in the F_1 and in the F_2 there is a clear cut 3 : 1 segregation of resistant to susceptible plants. In the F_3 generation therefore it is possible to obtain lines true breeding for rust resistance equal to one-quarter of the number of F_2 plants grown. This means that large numbers of resistant strains can be produced at will from which a rigid selection can be made of those possessing desirable agronomic characters and good milling quality. The inheritance of seedling resistance is much more complicated and since there are no varieties of *vulgare* resistant to the whole group of forms, the process of building up complete resistance by repeated crosses would be enormous.

It remains only to consider the nature of mature plant resistance and whether or not it will meet the requirements in the production of a rust resistant wheat. In the first place is it likely to continue to apply to all of the physiologic forms? Previous mention has been made of the variety Velvet Don which according to Aamodt (*2*) has been highly resistant in the rust nursery at University Farm, Minnesota, for 18 years. This variety was found to be susceptible in the seedling stage to 11 common physiologic forms so that it undoubtedly possesses a mature plant type of resistance. During the 18 years in the rust nursery at University Farm rust forms were used which were collected from all over the wheat growing area of the North-west so that forms to which Velvet Don is susceptible in the seedling stage must certainly have been present. The same is true of Acme wheat which has never been known to show an appreciable amount of rust in the field and yet in the seedling stage it is susceptible to every form to which it has been tested. The Marquis × Emmer lines, H-44-24 and Hope produced by Mr. McFadden are repeating the performance of Velvet Don and Acme. While susceptible to a number of forms in the seedling stage they are practically immune in the field. Clark and Ausemus (*3*) studied the field reactions of Hope wheat in a number of crosses with susceptible and partially resistant wheats and made the following statement: "It seems certain that most wheat breeding for rust control in the immediate future will be for rust immunity, using Hope or related strains as the immune parent."

The only possible difficulty with respect to mature plant resistance would appear to be its association with certain undesirable characters. In the H-44-24 × Marquis cross mentioned above it was found that the *susceptibility* of H-44-24 to black chaff was closely linked with *resistance* to rust. This of course may be a genetic linkage—in fact the results to date, Goulden, and Neatby (*7*), indicate that this is the case and that the two characters may be separated by growing sufficiently large populations. Other characters such as weakness of straw seem to be associated with mature plant resistance but here again the linkage seems to be genetic. A number of lines have been selected which possess high resistance and satisfactorily strong straw.

Summary

1. Fundamental investigations bearing on the practical problem of breeding rust resistant varieties of wheat are reviewed briefly.
2. Cytological studies including chromosome counts and chromosome behaviour in interspecific crosses show that it is logical to expect that certain characters such as rust resistance can be transferred from the 28 to the 42 chromosome group.
3. In three distinct cases rust resistance has been transferred in practical experiments from emmers and durums to common wheats.
4. The discovery of physiologic specialization in *Puccinia graminis tritici* explained the lack of uniformty in varietal trials for rust resistance. These studies have been continued and show that we now have at least 50 distinct forms all of which must be taken into consideration in the breeding program.
5. Color mutations in physiologic forms of stem rust and the discovery of heterothallism are indications that the number of physiologic forms may increase indefinitely by natural processes.
6. Mature plant resistance exhibited by certain rust resistant varieties appears to apply equally to all of the known forms of rust. Its existence very largely offsets the alarming possibilities through natural increases in the number of physiologic forms.
7. The inheritance of mature plant resistance is entirely independent of seedling resistance, and is very simple in nature. It offers much greater possibilities in the production of resistant varieties than the building up of seedling resistance by a complicated series of crosses.

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